



# The Repeated Evolution of Behavior

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A major tool in the evolutionary biologist's kit is to study the repeated emergence of certain biological traits. Employment of this tool has allowed substantial recent advances to be made in understanding the adaptive molecular basis of certain key biological traits. However, behavior, one life's most pervasive, and complex traits, is not one. Here we review the concepts of repeated evolution and how they apply to behavior. We assess the distribution and evolutionary dynamics of known cases of repeated behavioral evolution and examine their prospects for success in identifying the genetic and mechanistic bases of behavior. We propose that studying adaptive radiations, such as that seen amongst the cichlids of Lake Malawi, will likely yield results quickly due to the tractability of genetic and comparative analyses. Finally we suggest some possible scenarios that might be observed in the pursuit of the adaptive molecular basis of behavior and advocate for research on a diverse number of case studies of behavioral evolution, allowing for a knowledge base from which general principles of behavioral evolution might be gleaned.

**Keywords:** animal behavior, behavioral evolution, malawi cichlids, adaptive radiations, repeated evolution

## INTRODUCTION

Biologists have long appreciated that the repeated emergence of traits can act as a window into the workings of natural selection and the evolutionary process (Simpson, 1953; Mayr, 1963; Endler, 1986). When similar features occur in unrelated species it suggests a form of regularity in the actions of evolution that are capable of overcoming the unique constraints imposed by each species' unique history (Vermeij, 2006). Accordingly, recurrence in evolution is becoming an increasingly popular tool for analyzing how evolution can act at different levels (e.g., genome, development, molecular pathways, cellular functions) to converge on similar phenotypes. Cases of recurrent evolution recently been used to make inferences about molecular and developmental architectures of certain traits, giving insights into the "predictability" of genetic and phenotypic evolution (Stern and Orgogozo, 2008; Stern, 2013). There are now numerous examples in which lineages possessing recurrently evolved traits have been exploited to identify the genetic basis of morphological, life history, and physiological traits (Gompel and Prud'homme, 2009; Martin and Orgogozo, 2009; Stern and Orgogozo, 2009). We argue that it is time for behavioral biologists to join in.

Researchers are increasingly recognizing that complex behaviors too undergo recurrent evolution, both within closely related adaptive radiations and across distant taxa (Johnson et al., 2009), and presumably involving the action of selection acting on one or several of many possible biological pathways, some of which are unique to behavioral traits (e.g., nervous system form and function). We contend that the first steps toward this goal will require identifying and evaluating instances of behavioral evolution that are amenable to integrative study incorporating molecular, developmental, neurobiological, behavioral, and ecological insights. To this end we examine here a number of reported cases of repeated behavioral evolution and propose that early successes are likely to be found in the study of closely-related, yet highly variable, radiations of species. We next focus on an example from our lab-the evolution of bower building in Lake Malawi

cichlid fish-to demonstrate the surprising amount of convergence natural behaviors are capable of achieving amongst these radiations. Finally, we explore biological scenarios possibly unique to behavioral traits that might arise from the study of these systems, with a specific focus on theoretical relationships between the genome, nervous systems, and phenotypes in the repeated evolution of behavior.

## REPEATED EVOLUTION: VARIETIES

The **repeated evolution** of traits (“homoplasy”), traditionally construed (Lankester, 1870), can arise through several channels: *convergent evolution*, *parallel evolution*, and **functional redundancy**. Convergent and parallel evolution have been historically discussed together while functional redundancy is a related, but relatively newer concept. To start, the distinction between convergent and parallel evolution historically depends on ancestry and its role in adaptation. A classic outline of this distinction comes from Simpson’s Principles of Animal Taxonomy (1961). Here parallel evolution is defined as “independent occurrence of similar changes in groups with a common ancestry and *because* they had a common ancestry.” In contrast, “convergence is the development of similar characteristics separately in two or more lineages without a common ancestry related to the similarity but involving adaptation to similar ecological status” (Simpson, 1961; Wood et al., 2005). Modern interpretations of this distinction define *convergent evolution* as occurring when species employ *different* genetic processes (due to divergent ancestry) to arrive at the same phenotype while *parallel evolution* produces share phenotypes from the *same* genetic processes (likely due to shared ancestry).

### KEY CONCEPT 1 | Repeated evolution

The evolution of traits shared among species that are not possessed by their common ancestor. As used here repeated evolution encompasses a variety of processes and definitions outlined in the main text and **Table 1**.

### KEY CONCEPT 2 | Functional redundancy

Convergence on a similar functional outcome through different phenotypic strategies.

Since Simpson much debate has occurred surrounding the relationship between convergent and parallel evolution. This owes largely to the fact that the original definitions predated the advent of modern molecular methods (Losos, 2011; summarized in **Table 1**). Recently authors have suggested replacing the terms with others, including repeated evolution (Gompel and Prud’homme, 2009; Ord and Summers, 2015), homoplasy (Wake et al., 2011), and phylogenetic replication (Kopp, 2009). Arendt and Reznick (2008), on the other hand, collapse the distinctions altogether under one banner- convergent evolution-arguing that the convergent vs. parallel split represents a false dichotomy. They contend that since closely related species can converge on phenotypes using *divergent* genetic mechanisms and vice versa it is often difficult, if not impossible, to assign an arrow of causality in assessing convergent and parallel evolution (Arendt

and Reznick, 2008). Similarly Losos (2011) demonstrates at least six varieties of convergence/divergence that can occur depending on the level of phenomena analyzed (i.e., developmental pathway, gene function, phenotype, etc.).

This movement toward consideration of recurrence at multiple levels reflects has benefited from advances in whole genome sequencing, phylogenomics, and molecular biology. For example Stern (2013) updates the definitions based on results from modern genetic mapping of convergent traits, suggesting that repeated evolution occurs either through convergence on the same genetic variant through *de novo* mutation (“parallel evolution”), shared inheritance of an ancestral polymorphism (“collateral evolution”), or through the introduction of an allele into a population through hybrid breeding (“hybridization”) and provides a number of examples from recent work for each. Similarly, other authors have begun to highlight numerous instances of recurrent evolution of *genomic* features, such as gene loss and duplication, related to certain traits (Maeso et al., 2012). We believe that it is desirable to incorporate such information into our understanding of recurrent evolution and in the development of models describing it. Yet, since very few convergent behaviors have been mapped to causal genetic loci, it is at the moment difficult to discuss repeated behavioral evolution using updated definitions such as these. We instead here opt to use “repeated evolution” to refer to the genetic and phenotypic phenomena that constitute the gradient between parallel and convergent evolution represented by these recent models (but in the final section will discuss the prospects for refining this usage).

Cases from morphology exemplify the diversity of repeated evolution. A prime example is image forming eyes where six types of eye, three with chambers and three that are compound have evolved (Fernald, 2006). The strong constraints imposed by collecting and focusing light have limited the solutions yet the outcomes serve their owners well. Another example is reduced pigmentation that has occurred several times across diverse vertebrate taxa and has led to the occurrence of dark and light morphs within natural populations (reviewed in Gompel and Prud’homme, 2009). Several of these populations have distinct genetic mechanisms driving pigmentation reduction have been identified including *Oculocutaneous albinism type 2* (*Oca2*) in cave fish (Protas et al., 2007), *Kit ligand* (*Kitlg*) in sticklebacks, and humans (Miller et al., 2007), and *Melanocortin 1 receptor* (*Mclr*) in a variety of mammals, reptiles, birds, and fish (Hubbard et al., 2010). Here unrelated taxa have arrived at common adaptive phenotypes that have arisen from different genomic contexts but use similar genetic mechanisms. In contrast, the recurrence of pelvic reduction in threespine sticklebacks, a very recent postglacial radiation of freshwater fish species (<12,000 years) that have repeatedly colonized similar niches within North American lakes (Schluter, 2000). Recurrent deletions of the same genomic element underlie the adaptive loss pelvic armor within disparate populations of this radiation (Chan et al., 2010). Here the same genetic mechanism is used to create a common adaptive phenotype.

The final concept, *functional redundancy*, represents cases in which species can use a variety of different mechanisms to achieve

**TABLE 1 | The language of repeated evolution.**

Sources	Dependent	Independent	Redundancy
Simpson, 1961	Parallel**	Convergent**	*
Alfaro et al., 2005/Wainwright et al., 2005		*	Functional redundancy
Arendt and Reznick, 2008		Convergent	*
Kopp, 2009	*	Phenotypic replication/Evolutionary metamodel	*
Gompel and Prud'homme, 2009		Repeated evolution	*
Wake et al., 2011		Homoplasy**	*
Losos, 2011			Many to one
Stern, 2013	Collateral by ancestry/hybridization	Parallel	*
Ord and Summers, 2015	Parallel	Convergent	Functional redundancy
		Repeated evolution	

Represented in the table is a sample of the terms used to describe repeated evolution beginning with a classical definition from the modern synthesis (Simpson, 1961) and including updated definitions based on contemporary molecular and developmental work. The distinction between shared and different ancestries is represented by the broad categories "dependent" and "independent" within which the various author's models are represented. For example, Losos (2011) describes multiple possible combinations of divergence and convergence based on which levels of phenomena are analyzed and is thus represented by six boxes, colored to represent a gradient of phenomena. "Redundancy" broadly categorizes the phenomena of functional redundancy which as a concept is somewhat less debated.

\*Denotes no new term is directly provided in source

\*\*Homoplasy, parallel evolution, and convergent evolution have each been used in the evolutionary theory literature for over a century and were not coined by the authors provided [for example "Homoplasy" is referenced in Lankester (1870) and Darwin used the term "convergent evolution" in Darwin (1871)].

the same functional outcome. In these instances the trait of concern may have been arrived at using totally divergent genetic, molecular, or physiological mechanisms. This is well represented by studies of variation in the skeletal morphology of fish from the family *Labridae*. Labrid fish species use a complex network of facial muscles for feeding that vary widely and are associated with adaptive patterns of prey use (Wainwright et al., 2004). The mechanical output of these muscles is measured by the Maxillary Kinematic Transmission Coefficient (Maxillary KT). Species with high Maxillary KT tend to feed on zooplankton and elusive fishes and shrimps while species with low Maxillary KT tend to feed on more stationary prey (Wainwright et al., 2005). Strikingly, high and low Maxillary KT values, and their associated feeding styles, can be arrived at through very different musculatures, thus demonstrating that "many" phenotypes might be leveraged to achieve "one" functional outcome (Alfaro et al., 2005; Wainwright et al., 2005). In this sense functional redundancy differs from convergence and parallelism in that the traits and the genetic mechanisms of concern need not be the same but rather the functional consequence of their actions.

Future work will illuminate the relative contributions of each form of repeated evolution in the context of behavior. The first step in this process, though, will be identifying clades that possess substantial variation in behaviors that show evidence of independent evolution. In the next section we assess a number of known examples that seem to fit this bill.

## THE LANDSCAPE OF REPEATED BEHAVIORAL EVOLUTION

If, as we suggest, behavioral biologists are to leverage the repeated evolution of behavior as a research tool what do they have to work with? We surveyed the literature for reports of repeated behavioral evolution, looking for cases that were backed by a phylogeny and in which transitions between behaviors

could be identified with some confidence. Assessing repeated behavioral evolution as a function of **Phenotypic transitions** is useful as it allows inferences to be made about the genetic and adaptive landscapes within which traits have evolved. For example, a behavior that has arisen 30 times in a short time period presumably has very different molecular and evolutionary bases than one that arose only twice in distantly related taxa (the study of both being valuable in the developing a body of evidence of behavioral evolution). We sought to address two questions: First, to what extent has repeated behavioral evolution occurred taxonomically and, second, how is its occurrence distributed across evolutionary time? Answers to these questions could provide insight into the relative impact of different types of repeated evolution (e.g., within closely related species or amongst distantly related taxa) and potentially when and where to expect it.

### KEY CONCEPT 3 | Phenotypic transitions

An instance of repeated evolution within a phylogenetic context.

In total we collected 49 reported instances of repeated behavioral evolution across 39 taxonomic groups (Table 2). For each instance we recorded the estimated clade size, the hypothesized mechanism of repeated evolution, and the divergence time between representative species. The divergence times and taxonomic distances of the collected traits span wide distances, from ecological time scales within populations (e.g., Trinidadian guppies; Schwartz and Hendry, 2007) to >800 MYA splits between kingdoms (e.g., Mussels/tunicates; Koehl, 1996). In addition repeated evolution has occurred for a variety of behaviors, from social organization in fire and alpine silver ants (Purcell et al., 2014) to individual motor ability in Hawaiian gobies (Blob et al., 2006), and can be seen across animal phyla.

Plotting phenotypic transitions and divergence time reveals the landscape of repeated behavioral evolution (Figure 1). The

**TABLE 2 | Examples of repeated behavioral evolution.**

Taxonomic distance	~Divergence (MYA)*	Organism (common name)	# Transitions**	# Species/populations	Trait	Sources
Species/population	0.001	Trinidadian guppies	6	6	Female preference	Schwartz and Hendry, 2007 <sup>+</sup>
Species/population	0.005	Alewife	3	14	Foraging	Palkovacs et al., 2008 <sup>+</sup>
Species/population	0.01	Yellow wagtails	2	13	Song complexity	Ödeen and Björklund, 2003 <sup>+</sup>
Species/population	0.1	Cave mollies	2	2	Shoaling	Plath and Schlupp, 2008 <sup>+</sup>
Species/population	0.5	Green lacewings	2	2	Courtship song	Henry et al., 1999
Genus	1	Damselflies	4	4	Predator avoidance	Stoks et al., 2005 <sup>+</sup>
Family	2	Hawaiian gobies	2	3	Locomotor style	Blob et al., 2006 <sup>+</sup>
Genus	3	Stick insects	4	160	Plant preference	Soria-Carrasco et al., 2014 <sup>+</sup>
Species/population	3	Cave fish	At least 3	29	Sleep loss	Duboué et al., 2011
Species/population	3	Cave fish	2	29	Feeding posture	Kowalko et al., 2013
Species/population	3	Cave fish	3	29	Loss of schooling	Kowalko et al., 2013
Species/population	3	Cave fish	2	29	Loss of aggression	Elipot et al., 2013
Genus	4	<i>Tetragnatha</i> spiders	6	35	Web architecture	Blackledge and Gillespie, 2004
Clade	5	Malawi cichlids	Possibly > 10	200	Bower building	York et al., 2015
Genus	7	Crested/Thekla lark	2	2	Song	Laiolo, 2012 <sup>+</sup>
Genus	7	Orioles	8	25	Song	Price et al., 2007 <sup>+</sup>
Subfamily/tribe	7.4	Chats	5	39	Nesting material	Aliabadian et al., 2012 <sup>+</sup>
Subfamily/tribe	7.4	Chats	6	39	Nesting location	Aliabadian et al., 2012 <sup>+</sup>
Subfamily/tribe	7.4	Chats	8	39	Migratory behavior	Aliabadian et al., 2012 <sup>+</sup>
Family	10	Hydrobiid gastropods	8	27	Parental care	Haase, 2005 <sup>+</sup>
Family	15.1	Birds of paradise	7	156	Lekking	Irestedt et al., 2009b <sup>+</sup>
Family	20	Babblers	9	97	Domed nests	Hall et al., 2015
Family	30	Microhylid frogs	2	215	Parental care	Köhler and Günther, 2008 <sup>+</sup>
Family	30	Microhylid frogs	6	215	Froglet transport	Köhler and Günther, 2008 <sup>+</sup>
Family	30	Manakins	5	40	Display behaviors	Prum, 1990
Family	33	Ovenbirds/Woodcreepers	8	288	Nest building/Habitat use	Irestedt et al., 2009a
Genus	40	Anoles	2	12	Headbobbing	Ord et al., 2013 <sup>+</sup>
Family	40	Poison dart frogs	5	170	Parental care	Summers and Tumulty, 2014
Family	50	Damselfish	11	208	Feeding/farming	Frédérich et al., 2013
Genus	50	Drosophilid flies	6	1579	Mating in the dark	Markow and O'Grady, 2005
Genus	50	Drosophilid flies	5	1579	Male display	Markow and O'Grady, 2005
Genus	50	Drosophilid flies	At least 5	1579	Female courtship	Markow and O'Grady, 2005
Genus	50	Drosophilid flies	3	1579	Female remating	Markow and O'Grady, 2005
Family	53	Flea beetles	10	~15,000	Anti-predatory jumping	Ge et al., 2011 <sup>+</sup>
Order	53	Bats	2	~800	Echolocation	Jones and Teeling, 2006
Family	80	Mecysmaucheniid spiders	4	25	Power-amplified striking	Wood et al., 2016
Family	85	Mormyrid fish	2	~200	Electric signaling	Carlson et al., 2011
Order	90	Bees	6	~20,000	Eusociality	Danforth et al., 2006
Family	100	Aphids	At least 6	~4,700	Production of soldiers	Stern, 1994
Family	110	Weakly electric fish	2	~350	Jamming avoidance response	Bullock et al., 1975
Family	112	Fire ants/Alpine silver ants	2	~20,000	Social organization (polygyny)	Purcell et al., 2014
Clade	125	Nudibranchs	Up to 16	2000–3000	Swimming style	Lillis and Katz, 2013
Family	140	Araneoid spiders	16	16	Male genital mutilation	Miller, 2007
Class	250	Hymenoptera	11	~150,000	Eusociality	Woodward et al., 2011
Clade	300	Birds/Mammals	7	15,372	Vocal learning	Petkov and Jarvis, 2012
Kingdom	550	Insects/Mole rats/Shrimp	17	> 1,100,000	Eusociality	Jarvis et al., 1994; Duffy et al., 2000
Kingdom	847	Mussels/Tunicates	2	~65,000	Competitive dominance	Koehl, 1996 <sup>+</sup>
Kingdom	847	Birds/Fish/Insects	At least 10	> 1,100,000	Brood parasitism	Cervo et al., 2004 <sup>+</sup>

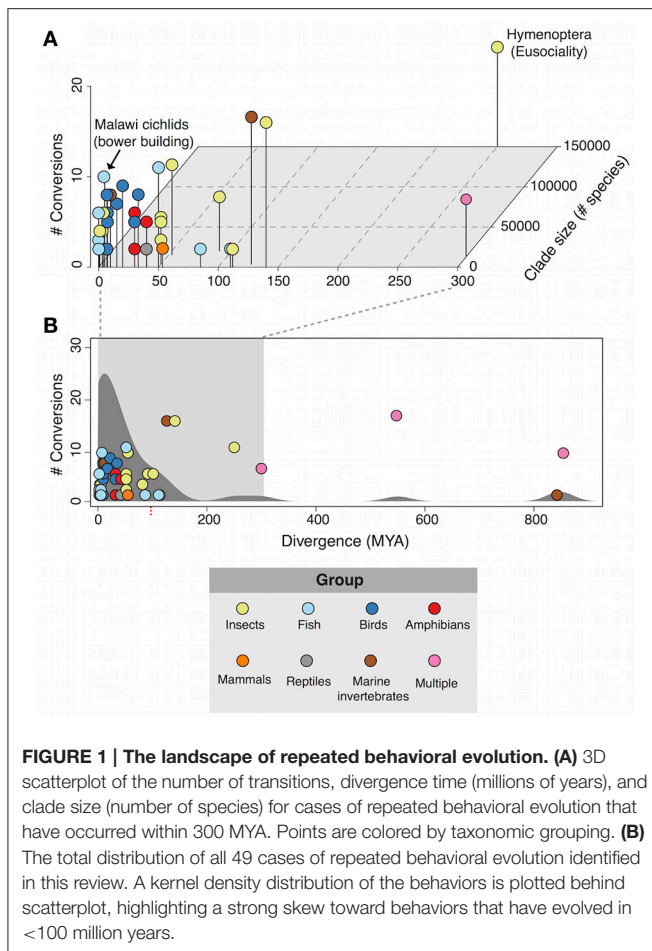
*Taxonomic distance, divergence time in millions of years, organism, number of transitions (instances of repeated evolution), number of species or populations, the behavioral trait, and source are reported for 49 cases of repeated behavioral evolution across 39 groups.*

*\*Divergence times in millions of years were, where possible, collected from the primary literature. If estimates did not exist timetree (<http://www.timetree.org/>; Hedges et al., 2006) was used to measure the divergence between the two most distantly related members of the focal clade.*

*\*\*The number of transitions for each case was either pulled directly from the original source or estimated from the reported phylogenies.*

*<sup>+</sup>Originally collected in Ord and Summers (2015).*





first major feature of the landscape is that there are several of instances or repeated evolution with more than 10 conversions including the evolution of bower building in cichlid fish (likely >10 conversions; York et al., 2015) and eusociality across invertebrates and vertebrate taxa (17 conversions; Duffy et al., 2000). A density distribution of repeated behavioral evolution instances across evolutionary time (Figure 1B) shows a skew toward more recent evolutionary events with the majority of <100 MYA (39/49; 79.59%). Furthermore, more than 80% (40/49) of cases occur at sub-family taxonomic units (species/genus/subfamily/family). Previous observations of repeated evolutionary events across other traits including morphology, physiology, and life history shows a similar trend, indicating that behaviors are not subject to evolutionary processes distinct from these other phenotypes (Vermeij, 2006; Ord and Summers, 2015).

In addition we find a significant positive correlation between clade size and conversion number ( $r^2 = 0.46$ ;  $p = 0.001$ ) but not between evolutionary divergence time and conversion ( $r^2 = 0.11$ ;  $p = 0.46$ ). This suggests that the probability of repeated behavioral evolution occurring may be driven more by clade size rather than evolutionary time. This point is may have some bearing on the consideration of when and where repeated behavioral evolution is expected to occur since evolution can

produce speciose clades in a variety of ways and on a number of time scales, a particularly striking example of which is the case of adaptive radiations (discussed below). If a major determinant of repeated behavior evolution is the sheer number of species a related group then it may be reasonable to expect an enrichment of repeated evolution amongst rapidly radiating groups of species.

It is important to note, though, that at the current moment it is difficult to disassociate the observed patterns from the influence of ascertainment bias and the complexity of identifying behavioral homologies between distantly related taxa. For example, it is possible that the current known cases of repeated behavioral evolution were arrived at due to their ease of study, be it through a ready ability to identify behavioral homologs or through rapid observation and measurement of the traits. Furthermore, there is a presumable multitude of other repeated behavioral evolution instances that we have not included here due to a current lack of knowledge regarding phylogenetic relationships and behavioral definitions. Notable in this list is the perceived repeated evolution of complex social behaviors across animals, especially in relation to the structures and strategies of parental care (Hofmann et al., 2014). Future work resolving the phylogenetic, molecular, and phenotypic bases of complex behaviors such as these will be illuminating and will aid in identifying the extent to which behavioral homologies may exist across taxa. To this end, and influenced by the history of identifying such phenomena in morphology, we propose that early successes may come if a focus is placed on clades that are speciose, diverse, and closely related, qualifications that are well met by the occurrence of adaptive radiations.

## ADAPTIVE RADIATIONS AS A FIRST STEP

**Adaptive radiations** (ARs) provide examples of the extreme “parallel” end of the repeated evolution spectrum. ARs are rapidly evolving lineages that arose from a common ancestral source and display substantial ecological and phenotypic diversification (Simpson, 1953; Schluter, 2000). Repeated evolution within adaptive radiations is presumably often due to convergence on a particular allele of an ancestral polymorphism, as is the case in the evolution of stickleback body armor (Colosimo et al., 2005). This need not always be the case and indeed examples exist of closely related populations using different genetic and developmental pathways to reach the same phenotype as has occurred in differentially pigmented populations of oldfield mice (Hoekstra et al., 2006) and cave fish (Wilkens and Strecker, 2003). A

### KEY CONCEPT 4 | Adaptive radiations (ARs)

The rapid diversification of a species arising from a common ancestral source, often due to novel environmental pressures and opportunities.

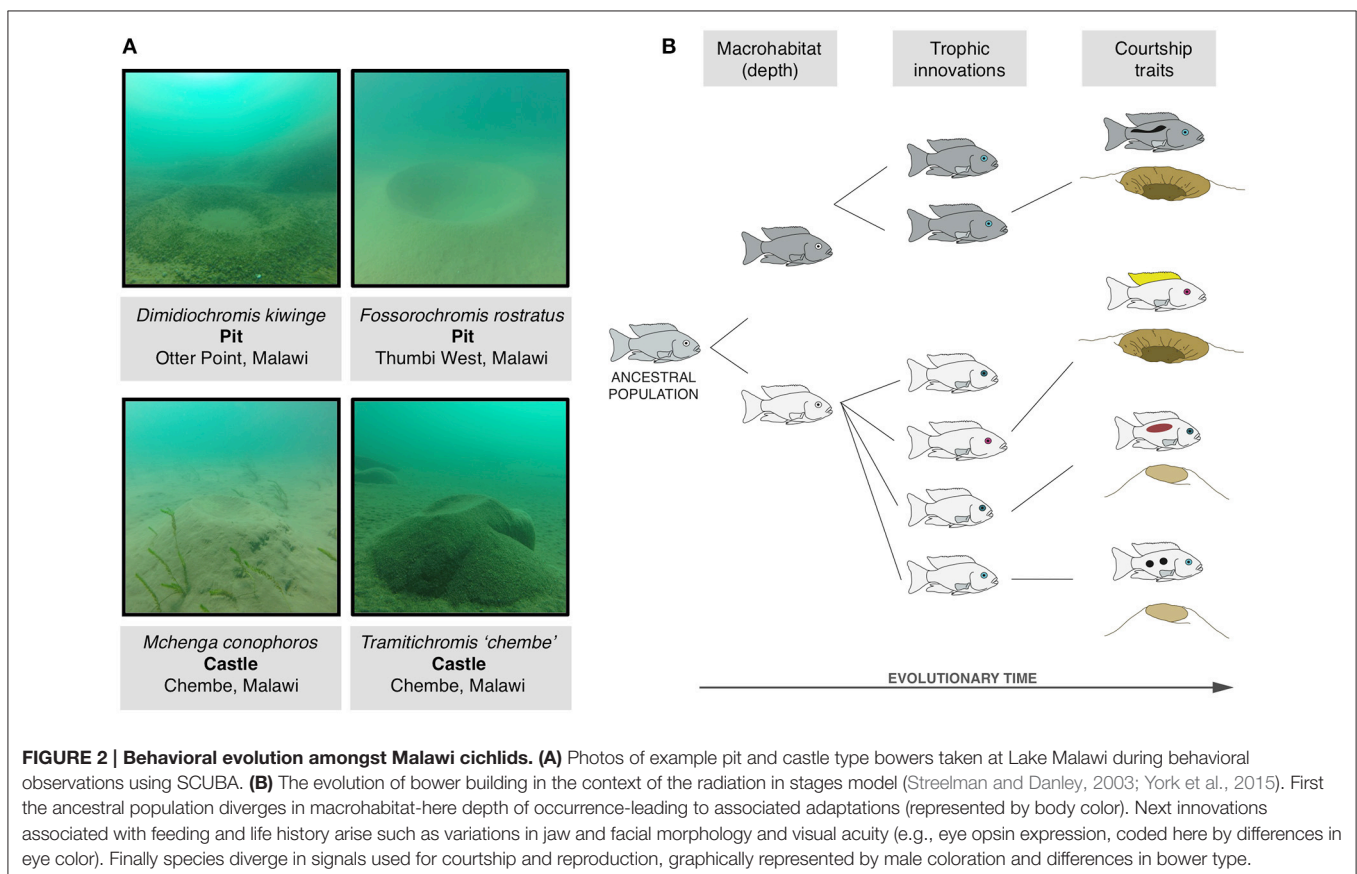
common method for conceptualizing macroevolutionary change in ARs is the “radiation in stages” model (Streelman and Danley, 2003; Gavrillets and Losos, 2009). The model proposes that species diversification in ARs occurs in the order of (i) macrohabitat, (ii) microhabitat or trophic (feeding) specializations, and (iii)

species-specific traits that lead to nonrandom mating (i.e., signals such as nuptial coloration and courtship behavior).

In York et al. (2015) we provide evidence that amongst the cichlid fish of Lake Malawi, Africa adaptations arising from stages (i) (macrohabitat) and (ii) (trophic style) have influenced the evolution of a courtship signal: the construction of sand mating nests or “bowers.” Males of more than 100 species within the sand-dwelling lineage of Malawi cichlids seasonally build bowers in large aggregations (“leks”) solely in order to attract and mate with females, a purpose almost identical to that of the eponymous bowerbirds of Oceania (Diamond, 1986; McKaye et al., 2001; Magalhaes et al., 2013). Bowlers are extended phenotypes that can exist in two basic form: “pits”-depressions dug out of the sand substrate-and “castles”-aggregations of sand collected from around the bower area and deposited to create a mound (Figure 2A; Dawkins, 1992; York et al., 2015). Phylogenetic analysis shows that pit and castle type bowers are evolutionarily labile. A partial phylogeny of 75 species from the sand-dwelling clade over 20 conversions between pit and castle are present. The number of phenotypic transitions of bower type is currently speculative as the current tree only represents a subset of the sand-dwelling lineage (200+ species in total). Whole-genome phylogenetic analyses will help in the resolution of within-genera variation of bower type. Nevertheless, the pervasiveness of bower building in this clade and its phylogenetic lability is a striking example of the extremes of courtship behavior diversity.

Why then did pit and castle type bowers repeatedly evolve? Like all cases of repeated evolution there are at least two levels at which this question can be addressed. The first is concerned with the genetic and molecular mechanisms that produced the repeated evolution. The second is concerned with the ecological and evolutionary pressures that facilitated it. Addressing the role of genetic constraints on bower type is currently difficult (though efforts are underway to clarify this issue). On the other hand there is some clarification regarding the roles of ecology and phenotype in the evolution of bower building. First, bower type correlates with macrohabitat (depth of occurrence) wherein castle-building species tend to occur at significantly shallower depths than pit-digging species. Second, bower type is associated with differences in functional morphology and eye opsin expression, suggesting that adaptations for specific diets, and trophic environments influence the propensity to build a pit or a castle (York et al., 2015). Broadly speaking castle-building species tend to be shallow-living, possess vision acuities sensitive to UV-rich light environments, and are adapted to extracting mobile food sources from the water column while pit-digging species are distributed at deeper depths, do not have UV vision, and tend to extract food through biting and scraping (Figure 2B).

Given the observed convergence in diverse traits across macrohabitat, morphology, and behavior amongst Malawi cichlids it is tempting to consider their evolution as having occurred on a macroevolutionary adaptive landscape with



**FIGURE 2 | Behavioral evolution amongst Malawi cichlids. (A)** Photos of example pit and castle type bowers taken at Lake Malawi during behavioral observations using SCUBA. **(B)** The evolution of bower building in the context of the radiation in stages model (Streelman and Danley, 2003; York et al., 2015). First the ancestral population diverges in macrohabitat—here depth of occurrence—leading to associated adaptations (represented by body color). Next innovations associated with feeding and life history arise such as variations in jaw and facial morphology and visual acuity (e.g., eye opsin expression, coded here by differences in eye color). Finally species diverge in signals used for courtship and reproduction, graphically represented by male coloration and differences in bower type.

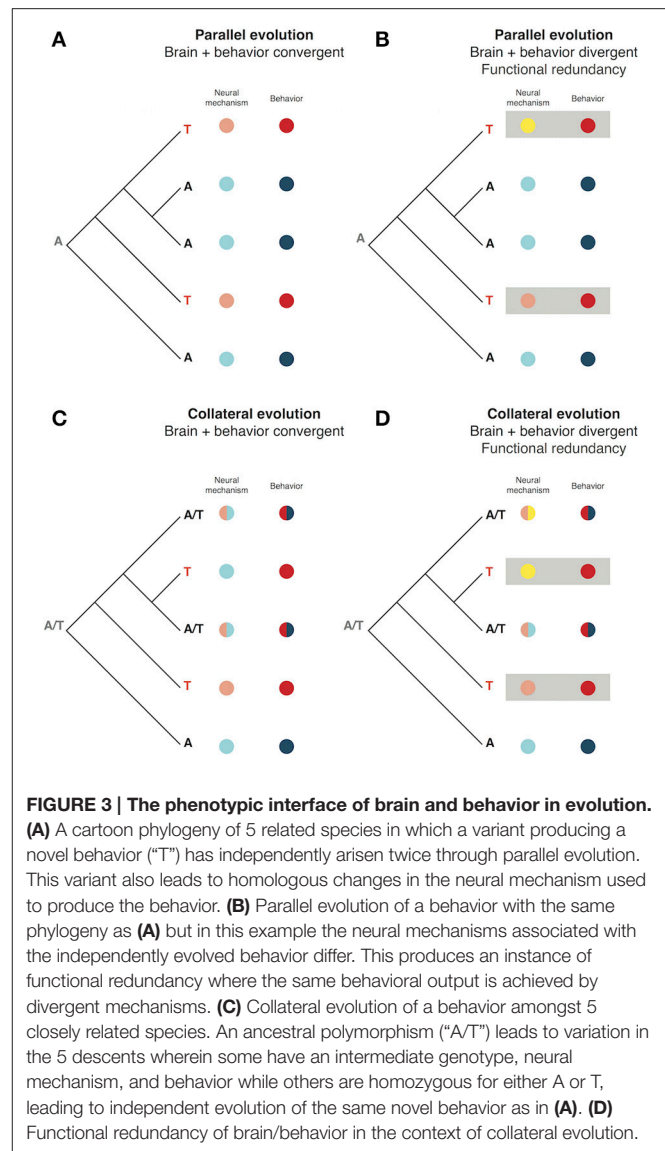
multiple peaks, each influencing and constraining the overall phenotypic makeup of individual species (Gavrilets and Vose, 2005). In such a case constraints imposed by the landscape will influence which species or lineages may or may not evolve certain traits. This has been observed in the evolution of the entire East African cichlid radiation variation in which both sexually selected traits *and* a variety of ecological factors predict whether or not species and lineages will radiate, indicating that certain clades may more prone to diversification and the evolution of specific traits than others (Wagner et al., 2012). This pattern suggests that similar adaptive landscapes exist across the lakes of Eastern Africa and has led to a process of replicated adaptive radiations in which common ecological pressures have led to phenotypic convergence across a number of them.

Other well-documented cases of such replicated ARs featuring behavioral convergence specifically have occurred in North American sticklebacks (Rundle et al., 2000), Caribbean *Anolis* lizards (Mahler et al., 2013), and Hawaiian spiders (Blackledge and Gillespie, 2004). Ecomorphs (phenotypes associated with distinct ecological niches) of Hawaiian orb-weaving spiders of the genus *Tetragnatha* show convergence of web architecture across the Hawaiian islands. Replicated ARs may hold great promise for the study of the behavioral evolution since they allow inferences to be made about the relative importance of non-behavioral factors (e.g., morphology, environment) on the phenotype of interest. Furthermore, ARs with cases of repeated evolution may offer unique opportunities to leverage population genetic methods for identifying the genomic basis of these traits, as for example has occurred for cichlid egg spots (Santos et al., 2014) and butterfly wing pattern (Reed et al., 2011) but has so far largely neglected physiological, life history, and behavioral traits (Berner and Salzburger, 2015).

## FUTURE PROSPECTS FOR BEHAVIOR EVOLUTION RESEARCH

Using the systems such as the ones described above researchers may soon begin to identify the mechanistic (genomic, molecular, phenotypic) bases of behavioral evolution. It will be illuminating to examine how these results compare to those obtained for other traits and to assay the extent to which behaviors are unique in their evolutionary patterns. We anticipate that one such idiosyncrasy will be the unique evolutionary relationship between the nervous system and the behaviors it produces. This is because, when selection acts on a behavioral phenotype, the genetic variants associated with that behavior most likely have their effects through nervous system structure and function. Barring future studies directly linking a gene with a specific behavioral phenotype it appears likely that this trend will become the rule.

The fact that behaviors are associated with variation in both the nervous system and the specific behavior trait itself differentiates them from other traits and may be unique to their evolutionary process. There may be several possible avenues through which adaptive variants in the genome may sculpt



behavior. Using models derived from known cases of the molecular evolution of morphological and life history traits, one can imagine hypothetical of cases parallel and collateral evolution (terminology from Stern, 2013) within a closely related group of species as examples. It is possible to schematize these scenarios (Figure 3). The first example demonstrates a case where two species have evolved a common behavioral phenotype arising from an identical genetic mutation (parallel evolution) that has its effect through the same neural mechanism (Figure 3A). It is also theoretically possible that, while both species share the same genotype and behavior, due to other evolutionary processes the neural mechanism associated with the behavior differs (Figure 3B). This case of parallel evolution may be seen as also incorporating an aspect of *functional redundancy* much like that seen in the feeding styles of Labrid fish discussed above. The same dichotomy between nervous system/behavioral convergence and divergence with functional



redundancy can also be considered for collateral evolution, either arising from shared ancestry or hybridization (Figures 3C,D; Stern, 2013).

When taking into account other biological processes such as development and gene function it is likely that the evolution of behaviors will not fall into this clean of a dichotomy (see Losos, 2011). What will be needed is the aggregation of case studies that tract the evolution of diverse behaviors across taxa and through time, from the genome through development to brain function and ultimately behavior. With these empirical data in hand researchers may begin outline general integrative principles of how and when behaviors evolve, thus allowing this trait to take its place alongside others in the pantheon of evolutionary analysis.

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## AUTHOR CONTRIBUTIONS

RY conceived of the manuscript idea and performed meta-analyses. RY and RF wrote the manuscript.

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